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SOME EXPERIMENTS IN MASS SELECTION

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AT the close of an interesting review of "seventeen years selection" of the character winter egg production in Barred Plymouth Rock fowls, made at the Maine Agricultural Experiment Station,¹ Dr. Pearl compares his results with those of Phillips and myself² in selecting for a like number of generations the hooded pattern of rats and concludes that the same interpretation should be given to both series of experiments, viz., that selection can change a population but not a character.

Without discussing for the moment the validity of the now world-famous generalization of Johannsen, which Pearl here accepts for his fowls and seeks to extend to our rats, I wish to point out some differences between the two cases which make a direct comparison between them difficult and conclusions based upon them of unequal validity.

The character winter egg production in fowls is on Pearl's showing extremely difficult to determine. It is necessarily an unknown quantity in all male birds, which themselves produce no eggs, and any influence which

¹ "Seventeen Years Selection of a Character Showing Sex-linked Mendelian Inheritance," AMERICAN NATURALIST, Vol. 49, pp. 595-608, 1915.

² "Piebald Rats and Selection," Publ. No. 195, Carnegie Institution of Washington, 1914.

males may exert on the egg-production of their daughters can be tested only by an indirect and rather uncertain process. Only in the case of females is the character directly measurable and then only for such females as (1) are hatched "after April 1 and before June 1," (2) survive all the accidents of chickhood and adolescence, (3) escape all attacks of disease and are kept continuously free from parasites, and (4) are properly fed and housed. For any bird which dies, is disabled or becomes seriously ill under ten months old, the character is an unknown quantity. These limitations make the proportion of birds which can be accurately rated as regards the character extremely small, and reduce correspondingly the material on which selection can be practised.

Contrast with this situation that regarding the hooded pattern of rats. This character is possessed by every individual of both sexes and is inherited equally through either sex. The character is fully developed in its final form within a week after birth, months before sexual maturity is attained. This makes it possible to grade the animals accurately while they are still very young and to discard at once all individuals which fall below the adopted standard. Selection thus has a vastly greater amount of material to work with, and the variation in each generation can be ascertained with a completeness and accuracy quite impossible in the case of winter egg production in fowls.

It is scarcely necessary to point out that upon the completeness of one's knowledge of the character and extent of variation depends his ability to take advantage of that variation by systematic selection. By this criterion winter egg production is very poor material on which to base an experimental test of "mass selection," whereas the hooded pattern of rats is material admirably adapted for the purpose. Many times has the fact been commented upon that Mendel's fortunate choice of peas as material for his studies of hybridization was largely responsible for his success where others failed. If one wishes to test

a theory he must choose material suited to the purpose. No adequate test of the efficacy of mass selection can be obtained from material which can not be accurately judged in the mass.

Pearl points out further limitations of his material in the statement "that phænotypic variation of the character fecundity, in fowls, markedly transcends, in extent and degree, genotypic variation." That is, non-heritable causes of fecundity are in excess of heritable causes and serve to obscure the occurrence of the latter. Further, Pearl says:

It is quite impossible in the great majority of cases to determine with precision what is a hen's genetic constitution with respect to fecundity from an examination of her egg record alone.

If then one has reared his pullets to the age of one year, has kept them free from disease and parasites, has fed and housed them properly and has even trap-nested them and recorded their eggs all winter, still he has no sufficient basis on which to base a selection. He must first rear and test their progeny in the same way. Pearl's statements on this point, the accuracy of which I do not question, are sufficient to show the entire unsuitability of his material for testing the efficacy of mass selection.

One might with propriety even question whether such a thing as inherited capacity for winter egg production exists in fowls, but on this point, I think, another investigation³ made by Pearl is conclusive, in which he crossed Cornish Indian game fowls, which are poor winter layers, with Barred Plymouth Rocks which are fairly good winter layers. Reciprocal crosses were made in both of which the daughters showed resemblance to the racial winter egg productiveness of the sire's race. This result indicates that a sex-linked genetic factor of some sort exists which affects winter egg production in fowls. But since the fecundity of the offspring was obviously influenced by the mothers' race as well as by the father's race, Pearl was

³ "The Mode of Inheritance of Fecundity in the Domestic Fowl," *Jour. Exp. Zool.*, Vol. 13, p. 153, 1912.

led to suggest the existence of a second fecundity factor which was *not* sex-linked. He assumes that this second factor, like the first, is a Mendelizing factor, but without any sufficient published evidence for either conclusion. To this I called Dr. Pearl's attention soon after the publication of his paper and suggested that if possible the data be put on record in such form as to allow of testing this and other hypotheses concerning the genetic factors concerned. For one-factor, two-factor, ten-factor and infinity-factor Mendelian hypotheses would call for very different ratios and distributions of fecundity among the offspring. He replied that the data could not be so given without an amount of work which he considered unprofitable. We are left, therefore, with only this information concerning Pearl's pullets, whether each one laid *more* or *less* than 30 eggs in its first winter. If we knew *what* number each one laid, we might form an intelligent opinion as to whether Mendelian factors are involved, and if so how many, in the same way that we can test Mendel's conclusions concerning the independent inheritance of yellow cotyledon color and round seed form in peas because he tells us the actual proportions of the various sorts of peas reported for each plant. Being denied such information by Pearl, it is useless to discuss his two-factor hypothesis, for its correctness can be neither proved nor disproved.

Leaving aside the question whether any inherited *factor* has changed as a result of selection in Pearl's experiments, which we have no means of investigating, we can consider only the question whether the gross winter egg production has changed. As a basis for judgment he gives us the averages of winter egg production year by year for sixteen years. Pearl's graphic presentation of the data (assuming that the considerable fluctuation recorded is not significant) indicates a steady decline of the general flock average during the first nine years of the experiment and a steady recovery and further increase during the next seven years, which he ascribes to

the different basis of selection in the two periods. But it is hard to believe that this entirely explains the difference in result. One notices for example that during the period of ostensible decline the highest average fecundity (45.23) is recorded when the number of birds under observation is smallest (48) and the lowest average (19.93) is recorded when the flock is largest (780). Further, in the later seven-year period of "improvement," the number of birds tested declines as their average fecundity rises. Has not the better environment and lessened competition of small numbers possibly something to do with the changes noted? Is it certain that genetic agencies are responsible for the differences observed? Pearl himself nowhere states that the selection practised during the earlier period had produced positive deterioration; he merely states that "there was no change of the mean in the direction of the selection" during this period when selection was based on high production without progeny tests. But as soon as progeny tests were made an additional feature of the basis for selection Pearl notes immediate results, viz., the immediate isolation of a strain which in its first year made a record for high productiveness only once equalled in the six subsequent years. How many successive selections were made in this period, we are not informed, but since it would require at least two years to make a combined performance and progeny test, it would seem that not more than three successive selections can have been carried out on this basis in the seven year period from 1908 to 1915. It may fairly be questioned whether this is an adequate test of the effectiveness of mass selection. The total number of individuals tested during this period is, according to Pearl's table, 1,655. For the entire seventeen years of selection it is 4,842.

The total number of animals graded in our selection experiments with rats heretofore published is 20,645, and the number of generations involved 13. Since those figures were compiled, four additional generations of

rats have been reared in the straight selection series, bringing the total number of animals observed in this experiment up to 33,249, and the total number of generations of selections up to 17, numbers certainly more nearly justifying the term "mass selection" than those studied by Pearl. As no previous account of this experiment has been given to readers of the NATURALIST, a brief review of its salient features may be appropriate here.

Experiments made by MacCurdy and by Doncaster had shown that the hooded pattern of rats is a Mendelian recessive character dominated in crosses by the "self" or entirely pigmented condition of wild rats and of certain tame races. The F_2 ratio obtained in crosses between hooded and self rats is an unmistakable monohybrid ratio, viz., 493 hooded: 1,483 self, or 24.9 per cent. hooded. The hooded pattern is subject to slight fluctuations in the relative amounts of pigmented and unpigmented surfaces, and though these slight plus and minus variations are such as are usually disregarded in Mendelian analyses, MacCurdy's investigations had indicated that they are to some extent inherited. It was our purpose in starting the selection experiments to ascertain whether the observed fluctuations were capable of increase and summation through the action of repeated selection, a possibility denied for all such cases by de Vries and Johannsen on theoretical grounds and quite incompatible with notions prevailing then as to the "gametic purity" of recessives. This "pure line" idea Pearl still maintains on the basis of his observations of the winter productiveness of his pullets. But, as I have tried to show, his material is no more adequate than that of Johannsen, which involved no demonstrated Mendelian character whatever. For, though Pearl *assumes* that winter egg productiveness of fowls involves a "sex-linked Mendelian character" he has withheld from publication the only facts on which such an assumption may legitimately be based.

Our selection experiments with hooded rats began in

1907. The initial stock consisted of less than a dozen individuals all "pure recessives," which produced only "recessive" hooded young, in accordance with Mendelian expectation. But though all the young were recessive (hooded), all were not exactly alike, and to assist in their classification we devised arbitrary "grades" of increased (plus) or decreased (minus) pigmentation as compared with the *modal* (zero) condition in our hooded race. The scale of "grades" is shown in part in Fig. 1. It has

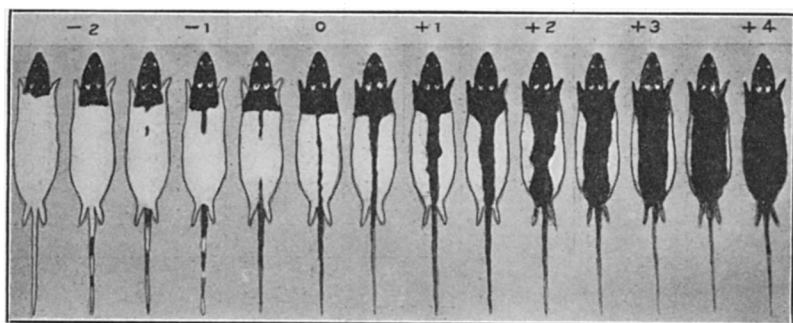


FIG. 1. Arbitrary set of grades used in classifying the fluctuating variations of hooded rats.

been found necessary to extend it in both directions, beyond the range shown in the figure, in order to admit the new grades of rats which have made their appearance as the experiment progressed. The first plus-selected parents produced 150 offspring ranging in grade from +1 to +3, mean +2.51. The first *minus-selected* parents produced 55 offspring ranging in grade from -2 to + $\frac{1}{2}$, mean -1.46. It will be observed that the ranges of the young produced in the two selections were practically continuous with each other, though they did not actually overlap. But actual overlapping did occur in the following generation, in which no advance was made in the mean grade of the parents, practically all the available females being used as parents in an effort to increase the stock. The grade of the offspring also remained practically stationary in this second generation (see Tables I

TABLE I

RESULTS OF THE PLUS SELECTION OF HOODED RATS CONTINUED THROUGH
SIXTEEN SUCCESSIVE GENERATIONS

Generation	Mean Grade of Parents	Mean Grade of Offspring	Lowest Grade of Offspring	Highest Grade of Offspring	Standard Deviation of Offspring	Number of Offspring
1	2.51	2.05	+1.00	+3.00	.54	150
2	2.52	1.92	-1.00	+3.75	.73	471
3	2.73	2.51	+ .75	+4.00	.53	341
4	3.09	2.73	+ .75	+3.75	.47	444
5	3.33	2.90	+ .75	+4.25	.50	610
6	3.52	3.11	+1.50	+4.50	.49	861
7	3.56	3.20	+1.50	+4.75	.55	1,077
8	3.75	3.48	+1.75	+4.50	.44	1,408
9	3.78	3.54	+1.75	+4.50	.35	1,322
10	3.88	3.73	+2.25	+5.00	.36	776
11	3.98	3.78	+2.75	+5.00	.29	697
12	4.10	3.92	+2.25	+5.25	.31	682
13	4.13	3.94	+2.75	+5.25	.34	529
14	4.14	4.01	+2.75	+5.50	.34	1,359
15	4.38	4.07	+2.50	+5.50	.29	3,690
16	4.45	4.13	+3.25	+5.87	.29	1,690
						16,107

TABLE II

RESULTS OF THE MINUS SELECTION OF HOODED RATS CONTINUED THROUGH
SEVENTEEN SUCCESSIVE GENERATIONS

Generation	Mean Grade of Parents	Mean Grade of Offspring	Lowest Grade of Offspring	Highest Grade of Offspring	Standard Deviation of Offspring	Number of Offspring
1	-1.46	-1.00	+ .25	-2.00	.51	55
2	-1.41	-1.07	+ .50	-2.00	.49	132
3	-1.56	-1.18	0	-2.00	.48	195
4	-1.69	-1.28	+ .50	-2.25	.46	329
5	-1.73	-1.41	0	-2.50	.50	701
6	-1.86	-1.56	0	-2.50	.44	1,252
7	-2.01	-1.73	0	-2.75	.35	1,680
8	-2.05	-1.80	0	-2.75	.28	1,726
9	-2.11	-1.92	- .50	-2.75	.28	1,591
10	-2.18	-2.01	-1.00	-3.25	.24	1,451
11	-2.30	-2.15	-1.00	-3.50	.35	984
12	-2.44	-2.23	-1.00	-3.50	.37	1,037
13	-2.48	-2.39	-1.75	-3.50	.34	1,006
14	-2.64	-2.48	-1.00	-3.50	.30	717
15	-2.65	-2.54	-1.75	-3.50	.29	1,438
16	-2.79	-2.63	-1.00	-4.00	.27	1,980
17	-2.86	-2.70	-1.75	-4.25	.28	868
						17,142

and II). In the third and all subsequent generations selection was made as rigorous as possible consistent with the maintenance of a strong colony from which to make further selections. Following each selection an advance in the average grade of the offspring took place attended by a steady movement in the direction of the selection on the part of both the upper and the lower limits of variation. The sixteenth plus selection produced 1,690 offspring (a larger number of individuals than is contained in Pearl's entire seven-year series) *every one of which fell beyond the original range of variation*, which was from $+1$ to $+3$ in the first plus selected generation and from $+3\frac{1}{2}$ to $+5\frac{1}{2}$ in the sixteenth generation. What this change signifies will be better appreciated when I state that $+6$ in our grades is a wholly pigmented or "self" rat, and that the extreme variation noted, $+5\frac{1}{2}$, signifies a rat wholly pigmented except for a few white hairs between the front legs. The *whole race* has accordingly been changed so that *no individual* is longer produced which falls within the original range of variation. Not a dozen rats in this entire generation would be allowed by a fancier in the category of "hooded" rats.

In the minus selection series the results secured are scarcely less striking. Only a very few individuals of the 1,980 sixteenth generation rats, or the 868 seventeenth generation rats fell within the original range of variation, which in generations 1-3 went no farther than grade -2 . In all other individuals of the sixteenth and seventeenth generations the "hood" was reduced to an extent never seen in the hooded rats of the fancier, the white areas having covered the neck and in extreme cases the forehead also, leaving only the nose and a patch round the eyes and ears still pigmented.

Pearl (p. 607) commenting on the results of his selections states that he had no reason to think that at the close of the series any individual had been produced superior in productiveness to those which occurred at the outset, but that he had merely secured *more of them*, thus raising

the average. With the rats, however, a very different condition exists. The average is not changed by increase of high-grade individuals merely or chiefly. At the present time *every individual* in the plus selection series and *nearly every individual* in the minus selection series is of higher grade (plus or minus respectively) than *any* individual in the race at the outset. It is not a fallacious change of averages which has taken place; a genuine and permanent racial change has occurred, following step by step upon repeated selection. Generation by generation new grades of offspring have come into existence, more extreme in character than any which existed before, and simultaneously with the advance of the outer limit of variation the inner limit has receded. No great change in variability has attended the selection. The standard deviation has decreased somewhat to about three fifths of its original amount, but has scarcely altered in the last eight or ten generations (see Tables I and II). Rather there has occurred a change in the *modal condition* of the character, about which fluctuation continues very much as before. When the position of the mode changes, as a result of selection, the position of the average and of the upper and lower limits of variation change with it. In a word the *character* changes.

In our 1914 publication Phillips and I were conservative about asserting a change in the single Mendelian unit-character manifestly involved in the hooded pattern. We suggested the possibility that other as yet undiscovered factors might be responsible for the apparent changes observed and awaited the result of experiments then in progress to show whether such a possibility was admissible. I have no hesitation now in saying that it is not. All the evidence we have thus far obtained indicates that outside modifiers will not account for the changes observed in the hooded pattern, itself a clear Mendelian unit. We are forced to conclude that this unit itself changes under repeated selection *in the direction of the selection*; sometimes abruptly, as in the case of our "mu-

tant" race, a highly stable plus variation; but much oftener gradually, as has occurred continuously in both the plus and the minus selection series. The permanency of these cumulative changes we have tested by repeated crossing of both selected races with the same wild race. The first cross seems to undo to a slight extent the work of selection, causing regression in both plus and minus selected races, but a second back cross with the wild race causes no further regression. Thus, plus-selected rats of mean grade 3.45 were crossed with wild rats and the recessive character was recovered in F_2 in 75 individuals, 24 per cent. of the entire generation. These 75 extracted hooded rats were of mean grade 2.89, a regression of .56 on the mean grade of their hooded grandparents, which is about double the regression shown by the plus selected race when not crossed with wild rats. It seems proper therefore to attribute to the wild cross a part of the regression observed in this case and this I have expressed by saying that crossing the selected race with wild rats tends to *undo* the work of selection. The suggestion was tentatively adopted by Phillips and myself that this *undoing* consisted in the removal of "modifiers" of some sort, possibly independent Mendelizing factors. If this explanation were correct, further crossing with wild rats should tend still further to "undo" the work of selection, so that ultimately the extracted hooded race should return completely to its original modal state, the zero grade. To test this matter, extracted hooded rats ranging from grade +2 to +4 (mean grade 3.01) were crossed back a second time with pure wild rats. The theory of independent modifiers would lead one to expect further regression as a result of this cross, but no regression was this time observed. Instead an advance of .32 took place bringing the mean of the twice extracted hooded recessives back to about the grade of the uncrossed race. The mean grade of the once-extracted grandparents, loaded in proportion to the number of their twice-extracted hooded grandchildren, was 3.01; the mean of the 263 hooded grandchildren was 3.33.

The number of these grandchildren is large enough to leave no doubt as to the conclusion that no further regression attended extraction of the hooded character a second time from the wild cross. The proportion of hooded individuals to non-hooded is also an unmistakable monohybrid ratio, viz., 263 hooded to 759 non-hooded, or 25.7 per cent. hooded in a total of 1,022 individuals.

This result indicates clearly the untenable character of our provisional hypothesis to explain the altered grade of hooded rats under selection and crossing, by invoking the action of independent modifying Mendelian factors. No evidence is forthcoming from further and more extensive experiments that such modifying factors are concerned in the result. It seems rather that the hooded character, which is a mosaic or balanced condition of pigmented and unpigmented areas, is slightly unstable. It oscillates regularly about a mean condition or grade, these oscillations being not phenotypic merely but in part genotypic so that selection brought to bear upon them is immediately and continuously effective.

There may exist cases of continuous variation purely phenotypic, as that of Johannsen's beans seems on his showing to be. In other cases phenotypic variations may so largely exceed genotypic variations that it is difficult to discover and isolate the latter, as has been Pearl's experience. But our experiments with rats show beyond reasonable doubt that genotypic variation, as well as phenotypic, may assume a continuous form, and if it does no one can question its further modifiability by selection. In denying effectiveness to selection in the case of continuous variation, it has been assumed, tacitly by DeVries and expressly by Johannsen, that continuous variation is wholly phenotypic. This assumption being disproved, the pure-line theory which rests upon it lacks adequate support.

It seems strange looking backward that the idea should have become so widely accepted that continuous or fluctuating variations are wholly phenotypic. For a continu-

ous variation signifies only the combined result of several independent agencies. In purely phenotypic variation (such as possibly Johannsen has observed) these agencies are obviously environmental and so do not affect the inheritance. But in a case of multiple genetic agencies (the existence of which everyone recognizes) a continuous series of variations may result which would be amenable to selection. Pearl and all other pure-line advocates admit the existence of such cases. But the same thing would result if, aside from purely phenotypic variations in a character, its single factorial basis should undergo quantitative variation. It is precisely this last named category of cases which alone can explain our rat results. And it is precisely this category of cases which the pure-line advocates, unable to disprove, boldly deny. Driven from all other defences they cling to this as their last line and solemnly repeat challenges issued years before in moments of greater confidence. Thus Pearl closes his paper with a renewal of the opinion expressed by him in 1912.

It has never yet been demonstrated, so far as I know, that the absolute somatic value of a particular hereditary factor or determinant (*i. e.*, its power to cause a quantitatively definite degree of somatic development of a character) can be changed by selection on a somatic basis, however long continued.

Our observations on rats are submitted as a sufficient answer to this challenge.

I do not suppose that Pearl means to be taken seriously when he says (p. 608) :

The extreme selectionist appears to believe that in some mysterious way the act of continued selection, which means concretely only the transference of each selected individual from one cage or pen to another to breed, will in and of itself change the germ-plasm.

I have never heard a selectionist, however extreme, express such a view; certainly I, whose views are attacked in the next sentence, have never entertained such an idea. But Dr. Pearl knows, as well as I do, that while the germ-plasm of the individual remains unmodified upon its trans-

fer from one cage to another, the character of the *germ-plasm of its descendants*, and so of the race, depends very largely upon what mates are transferred to the same cage with it. This is where the selection comes in and there is nothing "mysterious" about it either.

The idea that selection can bring about no change in the germ-plasm of the race "except by sorting over what is already there," to which Pearl gives expression, rests on the assumption that the germ-plasm never changes. What ground have we for such an assumption? No more than for the idea of the unchangableness of species, which formerly prevailed. Even Johannsen admits that large germinal changes ("mutations") *sometimes* occur. He himself records having observed them. Why should we be so skeptical about the occurrence of minor germinal changes? It is easy to overlook them when purely somatic changes are associated with them and outnumber them as they possibly do in Johannsen's beans and Pearl's fowls but a single clearly established case should suffice to establish their existence and their importance in evolution.